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Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border

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ABSTRACT

Most large mammalian carnivores are in global decline, largely due to their involvement in livestock depredation. Research that advances our understanding of predator–livestock interactions is crucial to conflict mitigation and carnivore conservation. Here we investigated the influence of environmental and socio-ecological factors on livestock depredation by carnivores in pastoral villages adjacent to the Maasai Mara National Reserve, Kenya during a 14-month period. We attempted to identify factors associated with temporal and spatial variation in depredation rates, incorporating data on a closely monitored spotted hyena (*Crocuta crocuta*) population known to be involved in depredation events. Spotted hyenas, leopards (*Panthera pardus*) and lions (*Panthera leo*) were responsible for 53%, 32%, and 15% of attacks on livestock, respectively. Monthly depredation frequency was correlated positively with rainfall and negatively with natural prey abundance. Radio-telemetry revealed that hyenas defending a group territory within the Reserve spent more time outside the Reserve during months when hyena attacks on livestock were most frequent. Results of logistic regression models, which indicated spotted hyenas were most likely to attack large villages, were supported by behavioral observations of hyenas near villages. Leopards however, selected villages that were spatially isolated from other villages. Hyenas were more likely to attack livestock enclosures constructed of local bush material than those of more sturdy "pole" timber, but use of pole material more than doubled the probability of leopard attack. Selection of fence type should therefore depend on the size and relative isolation of villages. Overall, improved fences, more watch dogs, and high levels of human activity were not associated with lower livestock losses to predators.

1. Introduction

Human activity has caused a global decline in many large carnivore species (Fuller, 1995; Nowell and Jackson, 1996). Although habitat conversion, declining natural prey populations, and commercial exploitation have contributed to carnivore losses, active persecution by humans, based on real or perceived threats to themselves and their livestock, appears to be the most important factor in observed declines (Woodroffe, 2001). Large carnivores, humans and their livestock have coexisted for millennia, but recent decades have seen dramatic increases in the frequency of

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human–carnivore conflict, resulting mainly from an exponential increase in the human population (Woodroffe, 2000; Conover, 2002).

Protected areas are fast becoming the last refugia for many large African predators (Mills, 1991), all of which have experienced significant declines in recent decades (Ginsberg and Macdonald, 1990; Nowell and Jackson, 1996; Mills and Hofer, 1998; Ogutu et al., 2005). However, even within protected areas, humans often remain the main source of mortality to large carnivores (Woodroffe and Ginsberg, 1998), with smaller reserves surrounded by dense human populations being particularly susceptible to species loss (Brashares et al., 2001; Harcourt et al., 2001). Because few of Africa's existing reserves are large enough to maintain viable populations of wide-ranging predators (Brashares et al., 2001), conservation of large African carnivores is likely to depend on networks of smaller reserves and private and communal lands, where successful conservation will be closely linked with an ability to resolve human–carnivore conflicts and minimize numbers of carnivores killed by people (Woodroffe, 2001). To this end, park managers, biologists, and indigenous people must coordinate efforts to understand the circumstances surrounding carnivore–livestock conflict, and combine empirical data with local experience to identify factors that may reduce its frequency (Treves and Karanth, 2003).

The Maasai Mara National Reserve, Kenya (hereafter the Reserve) is one of East Africa's most popular game viewing locations, largely because it supports a high density of large carnivores (Ogutu and Dublin, 1998; Ogutu and Dublin, 2002). In 1968, much of the communal land immediately north of the Reserve was opened to demarcation into group ranches (Kimani and Pickard, 1998), and by the late 1970s, all rangelands north of the Reserve had been assigned to group ranches, 4 of which currently surround the Reserve: Lemek, Ol Kinyie, Koyake and Siana. These rangelands effectively act as buffer zones, separating the protected Reserve from expanding commercial agriculture to the north and protecting known wildlife dispersal areas from habitat conversion (Serneels et al., 2001). However, as more ranches are lost to agriculture and human populations continue to grow (by an estimated 4.4% per annum on Koyake group ranch (Lamprey and Reid, 2004)), carnivore–livestock conflict is inevitable and likely to increase. To avoid the establishment of population "sinks" surrounding the Reserve, in which human-caused mortality limits survival of predators dispersing from the Reserve (Woodroffe and Ginsberg, 1998), livestock depredation and the resulting persecution of carnivores must be minimized.

Rates of livestock depredation by large carnivores can be influenced by local environmental conditions such as abundance of natural prey (Meriggi and Lovari, 1996; Mizutani, 1999; Stoddart et al., 2001; Polisar et al., 2003) and rainfall (Patterson et al., 2004; Woodroffe and Frank, 2005), as well as by socio-ecological factors including livestock husbandry practices (Meriggi and Lovari, 1996; Ciucci and Boitani, 1998; Stahl et al., 2001; Madhusudan, 2003; Ogada et al., 2003) and characteristics of attacked farms, villages, and livestock enclosures (Mech et al., 2000; Ogada et al., 2003). However, few studies have concurrently investigated the influence of both environmental and socio-ecological factors on livestock depredation, and even fewer have combined this knowledge with consideration of the behavior and movements of monitored predators. Our goal was to elucidate relationships between various ecological factors and temporal variation in conflict frequency in the vicinity of the Reserve, and to assess the influence of village and enclosure characteristics on relative vulnerability to carnivore attack. The concurrent long-term study of spotted hyenas (*Crocuta crocuta*) in our study region provided a unique opportunity to associate detailed data on hyena movements with hyena depredation behavior.

2. Methods

2.1. Study area

2.1.1. Geography and climate

Our study was conducted along the northeastern border of the Maasai Mara National Reserve (1500 km^2) in southwestern Kenya (Fig. 1). The portion of the study area outside the Reserve included sections of the Koyake and Siana group ranches, which share their southern borders with the northern border of the Reserve. The study focused on three adjacent locales within these ranches: Talek, Ntipilikwani, and Olosogon. These were chosen for their accessibility, and their relatively high density of settlements near the Reserve. The Talek region supports the highest density of settlements along the entire northern border of the Reserve (Reid et al., 2003). The dominant land uses on the group ranches are subsistence pastoralism and wildlife tourism. The eastern portion of the Reserve and environs receive approximately 600 mm of rain annually (Norton-Griffiths et al., 1975), most of which falls during one of two wet seasons: the "short rains" in November–December, and the "long rains" in March–May.

2.1.2. Wildlife and habitat

Both the Reserve and the surrounding group ranches support a large diversity of resident ungulates including gazelles (*Gazella thomsonii* and *G. granti*), impala (*Aepyceros melampus*), topi (*Damaliscus lunatus*), and giraffe (*Giraffa camelopardalis*). From August to October small resident populations of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) are joined by large migrant herds from Tanzania. It is estimated that 300,000–750,000 wildebeest enter the Reserve during the annual migration, with 50,000–150,000 spilling onto the four adjacent group ranches (Broton and Said, 1995; Ottichilo et al., 2000). The dominant predators in the Reserve are spotted hyenas, lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*). Although striped hyenas (*Hyaena hyaena*) occur in this region, they were not known to attack any livestock during the study period. Therefore, discussions of hyenas below refer exclusively to spotted hyenas.

The Reserve consists primarily of rolling grassland and scattered bushland (predominantly *Croton* sp. and *Euclea* sp.), with riparian forest along the major watercourses. The portions of the Koyake and Siana group ranches in our study area are grazed year-round by livestock, and include habitat similar to that of the Reserve, with somewhat reduced woody vegetative cover.

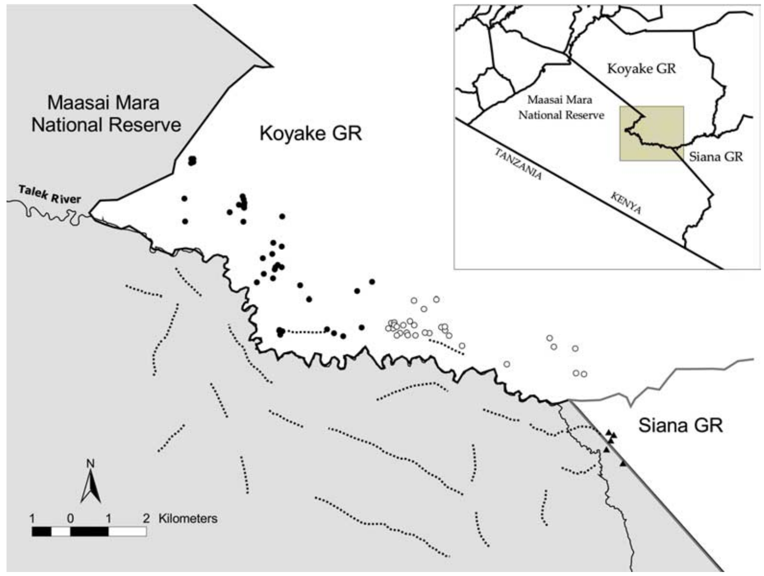

Fig. 1 – Locations of Maasai bomas (villages) of the Talek (filled circles), Ntipilikwani (open circles), and Olosogon (triangles) locales from which information on livestock depredation by large carnivores was collected from March 2003 to April 2004. Only bomas that contained livestock and were located within 2 km of the Reserve border are included. Dashed lines indicate prey transects.

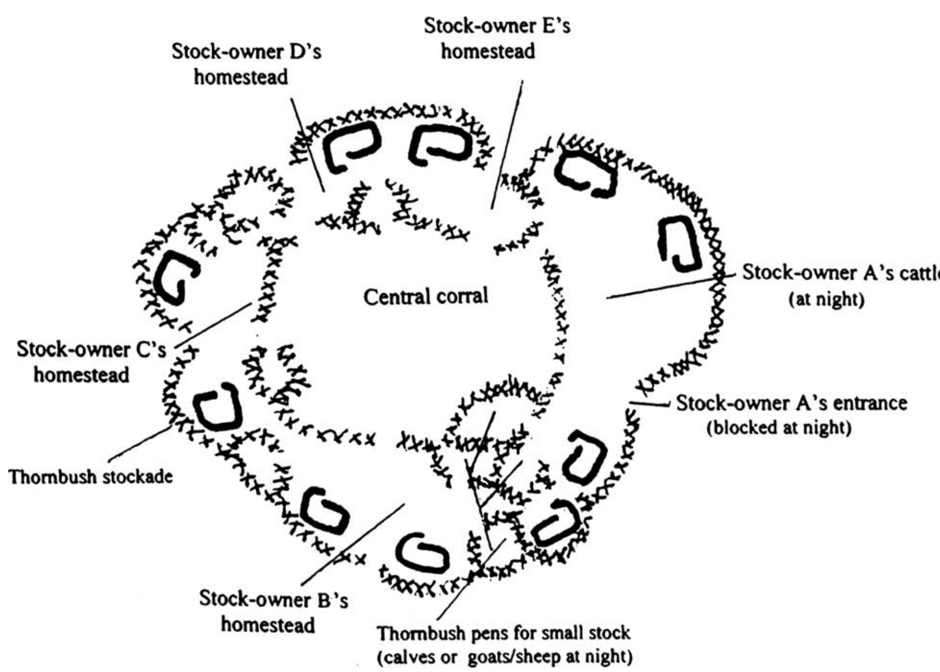

Fig. 2 – Configuration of a typical Maasai village (boma). Cattle from all household heads are housed together in the shared central corral. Individual homesteads maintain separate enclosures for their own small stock. Figure adapted with permission from Spencer (2003) p. 45.

2.1.3. The Maasai village

The traditional Maasai village, or boma, in this region consists of a collection of wooden-frame huts, covered with mud and dung, surrounding a central cattle enclosure (Fig. 2). A number of household heads may reside at a boma with their personal dwellings built in distinct sections of the boma. Each household head keeps his cattle in the shared central enclosure at night and maintains a separate enclosure among his huts, in which only his own sheep and goats are kept at night (Homewood and Rodgers, 1991; Burnsilver et al., 2003). In our study area, livestock enclosures were constructed of local bush (often thorned), or tall (1.5–2 m) pieces of split timber ("poles"), spaced up to 0.25 m apart, and sometimes fortified by chain link or barbed wire. Enclosures for sheep and goats were always more sturdy and complete than those for cattle. An additional small peripheral bush fence was often constructed around the entire boma compound (Fig. 2). Donkeys were rare in the region, but when present were usually kept within the peripheral boma fence at night.

Livestock were typically driven out of the boma between 08:00 and 09:00 hours for grazing and returned to the boma just before sunset. All herds outside of the boma are referred to here as grazing herds and were always monitored by one to several herders. Grazing cattle typically traveled 2–5 km from the boma, but sheep and goat herds rarely traveled more than 2 km. Illegal livestock grazing occurred within the Reserve, and sometimes occurred at night, when Reserve rangers rarely patrolled.

2.2. *Collection of conflict data*

In February 2003 we trained three Maasai scouts, one from each of the study locales, to complete a one-page report when notified of any injury or death of livestock deemed to have been caused by carnivores. We also held meetings with elders from each locale to discuss our project goals and request landowners to inform their local scout of depredation events occurring either at the boma or during grazing, as soon as possible after they occurred. It was widely known by local villagers that our research was not affiliated with the any government entity, and that we offered no compensation for depredated livestock. There was thus no apparent incentive for exaggerating or fabricating claims, but scouts nevertheless made every effort to confirm all incidents based on available evidence. Bomas more than 2 km from the Reserve were excluded to maximize efficient monitoring of the area by scouts. A few settlements that contained no livestock of any type were also excluded from the study. Conflict reports were collected from March 2003 through April 2004.

Based on available evidence and witness accounts, scouts recorded the time of day of each attack, the number and species of all livestock killed or injured in the attack, the predator species involved, and the nature of the interaction, if any, between villagers and the predator. A narrative account of each event was recorded, as was the evidence used to identify the predator species. We documented the number of cattle held in the central enclosure as well as the number of sheep and goats held in the owner's small stock enclosure. With the exception of the enclosures themselves, village residents and their domestic dogs are the only deterrents to predator attack at Maasai bomas. Neither firearms nor night watchmen are used in this region. We therefore recorded the number of dogs associated with each affected household as well as the total number of dogs at the boma. As an indicator of the level of human activity at attacked bomas, we recorded the number of household and total boma huts. Finally, we categorized the cattle and small stock enclosures as either pole fences, bush fences, or other. These same variables were also recorded for all bomas and enclosures that did not suffer any depredation losses during the study. A single observer (JMK) assessed the strength (strong vs. weak) of attacked and unattacked enclosure fences based on their relative levels of maintenance, reinforcement, and overall sturdiness.

The spatial locations of all study bomas and enclosures were recorded using a hand-held GPS unit. We measured the distance from each boma and enclosure to the nearest vegetative cover adequate to conceal a predator in daylight, because predators may be less willing to attack livestock further from cover. Because densities of some large predators are likely lower outside than inside protected areas (Mills and Hofer, 1998; Caro, 1999; Ogutu et al., 2005), bomas further from the Reserve may be less vulnerable to attack. We therefore measured the distance to the Reserve border for each study boma and enclosure using ArcView GIS 3.2 (Environmental Systems Research Institute, Redlands, CA, USA). Finally, the isolation of bomas relative to other bomas may also influence their vulnerability to attack. We therefore recorded the distance to the nearest boma, and the density of bomas within a 200 m radius of each boma. The same analysis was repeated using enclosure locations to characterize the relative isolation of individual sheep/goat enclosures. Accurate locational data were unavailable for attacks on grazing herds.

2.3. *Ecological conditions and predator movements*

Previous research has suggested natural prey abundance may influence depredation rates (Polisar et al., 2003; Woodroffe et al., 2005), and that rainfall may be an indirect measure of prey abundance and observed variation in depredation frequency (Patterson et al., 2004; Woodroffe and Frank, 2005). We therefore examined relationships between temporal variation in depredation frequency and both rainfall and prey abundance. Total monthly rainfall was measured using a standard metric rain-gauge located along the Talek River. We assessed the availability of natural prey to large predators by counting all prey occurring along 29 one kilometre road transects, two of which were located on group ranch property (Fig. 1). We counted all wild ungulates within 100 m of each transect 2–4 times per month for 13 of 14 months during the study period. An average number of ungulates counted per census was then calculated as an index of local prey abundance in each month.

We monitored radio-collared adult spotted hyenas throughout the study period to determine whether predator movements were associated with temporal variation in depredation behavior. Spotted hyenas live in social groups called clans and cooperatively defend a stable group territory. Monitored hyenas were members of a single clan whose northern territory boundary extended into the Talek and Ntipilikwani locales outside the Reserve, and whose 47–55 members were known to be involved in local depredation events. Between 2001 and 2005, at least nine clan members were killed at bomas within the study region during livestock attacks.

We documented hyena space use with two different monitoring techniques. The first method utilized frequent ($\sim$1 location per hyena every 2–3 days) telemetry locations collected at all times of day and night, with the majority of monitoring effort occurring near dusk and dawn. Three individual home-ranges (HRs) were constructed for each of 8 hyenas (4F, 4M) based on a minimum of 35 locations per hyena ($\bar{x} = 57$ locations) collected during months in each of 3 depredation categories. Months having <4 hyena attacks were classified as "low" depredation periods, between 4 and 7 as "mid", and >7 as "high". We then associated each depredation category with the proportion of each individual's corresponding HR situated outside the Reserve. All HRs were calculated with Animal Movement Analyst (Hooge and Eichenlaub, 2000) as 95% fixed-kernel utilization contours with smoothing factors (*h*) determined using least-squares cross-validation (Worton, 1989; Seaman and Powell, 1996).

Our second method utilized long-term (2–15 h) follows of 9 radio-collared hyenas (6F, 3M) conducted at all times of day and night. During follows, locations of the focal hyena were recorded every 10 min using telemetry, often with visual confirmation, to assess the frequency of use by hyenas of the group ranch properties outside the Reserve. The average proportion of locations per follow on ranch property was compared to the proportion of the clan territory extending into the ranches. The clan territory boundary was based on a 95% fixed-kernel utilization contour constructed using 4763 locations of 11 adult female hyenas collected from May 2002 to April 2004. Infrared spotlights and night-vision goggles were used to observe hyenas at night with minimal disturbance. Special attention was paid to the behavior of followed hyenas in close proximity to bomas or humans.

2.4. *Statistical analysis*

Data involving livestock losses and characteristics of attacks were summarized using proportions, which were compared between two groups using Fisher exact tests (Zar, 1999). Relationships between ecological variables and monthly attack frequencies were investigated using Pearson's correlation coefficients (r_p), with prey abundance data log-transformed to obtain normality. To identify whether hyena movements were associated with rainfall or prey abundance, we used these independent variables in a regression model with % of HR outside the Reserve as the dependent variable. For this model, locations from all monitored hyenas were pooled by month ($\bar{x} = 120$ locations per month, min = 74) to obtain a continuous monthly measure of clan space use. To associate hyena depredation behavior with hyena space use, average % HR outside the Reserve for individual hyenas was compared among the three hyena depredation categories using the non-parametric Friedman test for repeated measures.

We used univariate analyses to compare characteristics of bomas and enclosures that were attacked by predators with those of bomas and enclosures that were not attacked. Because most descriptive data for bomas and enclosures were not normally distributed we used Mann–Whitney *U*-tests to compare continuous variables between groups. We next used these descriptive variables in multivariate logistic regression analyses to determine which were useful in predicting probabilities of hyena and leopard attacks on both bomas and individual sheep/goat enclosures for a total of four model-building progressions. We first eliminated highly correlated continuous variables using Spearman rank order correlation coefficients (r_s) and excluded one variable from each correlated ($r_s > 0.70$) pair based on the results of exploratory univariate tests. All possible logistic regression models for each of the four dependent variables, utilizing all combinations of the remaining predictor variables, were then compared using Akaike's Information Criterion (AICc) values corrected for low sample sizes. Relative to the model with the lowest AICc value, models with a difference in AICc > 2.0 are considered to have substantially lower empirical support (Burnham and Anderson, 2002). We therefore considered all models within this range of the lowest AICc model. The significance of logistic regression models was assessed using a likelihood-ratio χ^2 test, while significance of model parameters was assessed using Wald's χ^2 test. All tests were considered statistically significant at $\alpha = 0.05$, and all analyses were conducted using the software package STATISTICA (StatSoft, 2002).

3. Results

3.1. *Losses of livestock and carnivores*

A total of 130 depredation events were recorded from March 2003 through April 2004. Every incident was attributed to a specific predator, with 71% based on visual confirmation of the predator, and the rest based on tracks, claw marks, or the condition of the livestock carcass. Hyenas were involved in 69 of the 130 reported incidents (53%), with leopards and lions involved in 32% and 15%, respectively. There were no reported depredation events involving other predators.

During attacks, carnivores killed 147 stock animals: 115 sheep and goats (78%), 30 cattle (20%) and two donkeys. Hyenas, leopards and lions were responsible for 50% ($n = 74$), 37% ($n = 55$) and 12% ($n = 18$) of the livestock deaths, respectively. Leopards accounted for 48% of all sheep and goats killed, but never attacked cattle. Lions killed only one goat, but accounted for 57% ($n = 17$) of all cattle kills. Sheep and goats comprised 80% of all livestock kills by hyenas. Hyenas were responsible for 51% and 43% of all sheep/goat and cattle depredation respectively.

Seventy-five (58%) of the 130 recorded attacks occurred inside bomas, with the remaining attacks directed at grazing animals. Hyenas attacked grazing herds as often as corralled herds (45% and 55%, respectively; Fisher exact test $p = 0.336$) and were responsible for more than 80% of attacks both on cattle within the boma, and on grazing herds of sheep and goats (Fig. 3). Lions attacked corralled livestock ($n = 2$) less than they attacked grazing herds ($n = 18$; Fisher exact test $p = 0.014$), and were involved in 74% of attacks on grazing cattle herds (Fig. 3). Conversely, leopards attacked grazing herds ($n = 5$) less than livestock in bomas ($n = 36$; Fisher exact test, $p = 0.0003$) and were responsible for 56% of all attacks on sheep and goats in bomas (Fig. 3). All attacks at the boma took place during the night whereas 71% of attacks on grazing herds took place between 11:00 and 16:00 hours.

Of 109 fatal attacks, 81% resulted in the death of only one stock animal, and 8% in the death of 3 or more. Most (76%) of the attacks on livestock in bomas were detected in progress, often resulting in the predator being chased from the scene. Undetected boma attacks were more likely than those detected to result in livestock death (100% vs. 79%, Fisher exact test, one-tailed $p = 0.027$). Attacks on livestock resulted in the confirmed death or injury of 4 hyenas and one lion.

The number of sheep and goats reported for 99 individual enclosures was estimated at 16,523. Thus, the 115 sheep and goats killed by predators resulted in an annual loss of 0.6% (98.4 animals) of the study region's small stock holdings. Considering only the 48 owners that suffered sheep or goat losses to predators, each suffered an average annual loss of 1.8% of

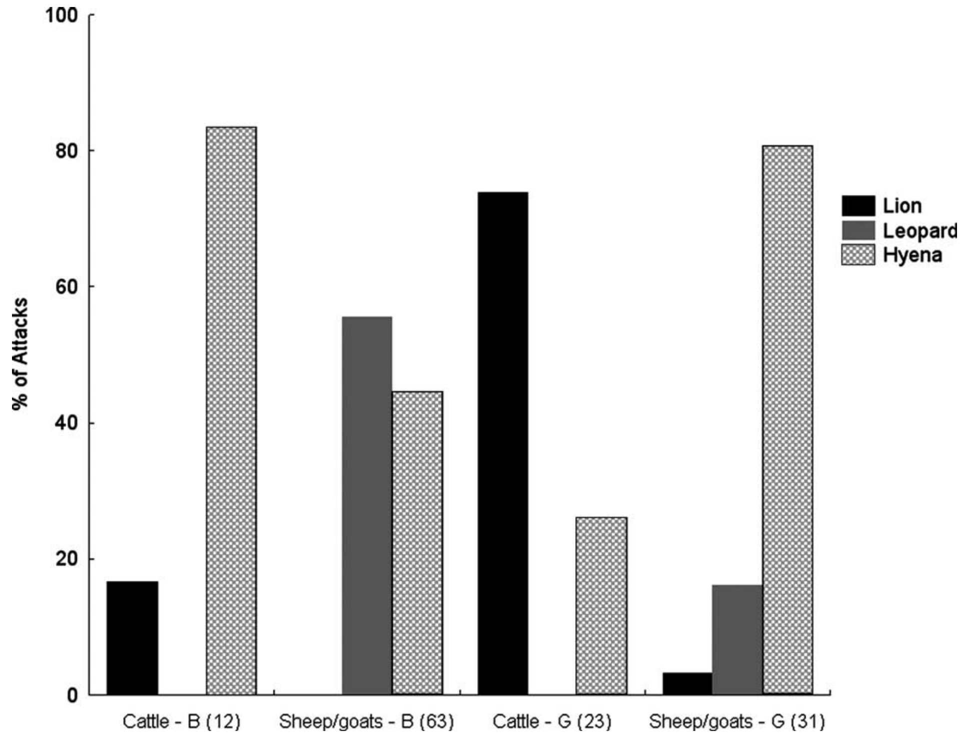

Fig. 3 – Involvement of lion, leopard and hyena in 4 categories of livestock depredation incidents along the northeast border of the Maasai Mara National Reserve during a 14-month study period. Total numbers of attacks of each type are listed in parentheses after category headings. "B" indicates attacks at the boma; "G" indicates attacks while grazing.

his stock (range: 0.2–8.6%). Given an estimated 11,864 cattle at the 78 study bomas, we recorded an annual loss to predators of 0.2% of the total cattle holding. Over a 14-month period, livestock depredation resulted in a loss of 6049 USD (460,000 KSh) to the study region. Hyenas were responsible for 45% of this monetary loss, lions for 36%, and leopards for 19%.

3.2. *Temporal patterns of attacks and relationship to predator movements*

There was substantial monthly variation in the number of depredation events, with attack frequency highest from March to May and lowest in October (Fig. 4). Monthly attack frequency was positively correlated with total monthly rainfall ($r_p = 0.66$, $p = 0.010$, $n = 14$; Fig. 5). In addition, monthly prey abundance was correlated with attack frequencies ($r_p = -0.67$, $p = 0.018$; $n = 12$ months) with October 2003 excluded. We excluded this month from this analysis because October prey counts failed to reflect the super-abundance of migratory prey present in the area. Although both variables were related to attack frequency, total monthly rainfall and average monthly prey abundance were not correlated ($r_p = -0.44$, $p = 0.149$; October excluded).

Space use by radio-collared hyenas was related to hyena depredation behavior. We found that the % of each hyena's HR falling outside the Reserve border was significantly higher in mid- and high-level depredation periods than in low-level periods (Friedman $\chi^2 = 12.0$, $p < 0.003$; Fig. 6). This variation was not likely to have resulted from changes in natural prey abundance outside the Reserve, as group ranch prey transects showed low monthly prey numbers ($\bar{x} = 2.4 \pm 3.4$ (SD)prey per transect), relative to inside the Reserve ($\bar{x} = 40.6 \pm 31.2$ prey per transect) throughout the year. Neither rainfall nor prey abundance was useful in predicting the % of monthly clan HR outside the Reserve ($F_{(2,10)} = 1.19$, $R^2 = 0.192$, $p = 0.344$).

We collected 1754 locations ($n = 811$ night, 943 daylight) during multiple follows on each of 9 different hyenas. Both nighttime ($n = 33$) and daytime follows ($n = 39$) provided an average of 24 locations per follow. Although 9% of the clan territory lay outside the Reserve, an average of 17% of locations per nighttime follow were outside the Reserve, yet only 0.4% of locations per daytime follow were outside the Reserve. Of the 130 locations outside the Reserve during follows, 23% were within 200 m of a boma. When outside the Reserve, followed hyenas were often seen foraging close to bomas, but making no attempts to enter them. In addition, our observations suggest that, at least in darkness, hyenas do not appear concerned about humans. Groups of hyenas sometimes slept for extended periods within 150 m of large bomas and hyenas were seen to walk calmly within 50 m of humans, only fleeing from those carrying flashlights.

3.3. *Characteristics of bomas and enclosures*

3.3.1. *Univariate comparisons*

Bomas that suffered at least one hyena attack differed from those that did not with respect to five of nine variables (Table 1). Bomas attacked by hyenas contained larger numbers of cattle, sheep and goats, sheep/goat enclosures, dogs and houses than did bomas not attacked by hyenas. All significant variables with the exception of the number of cows at the boma were intercorrelated ($r_s > 0.70$; Table 1). Bomas suffering

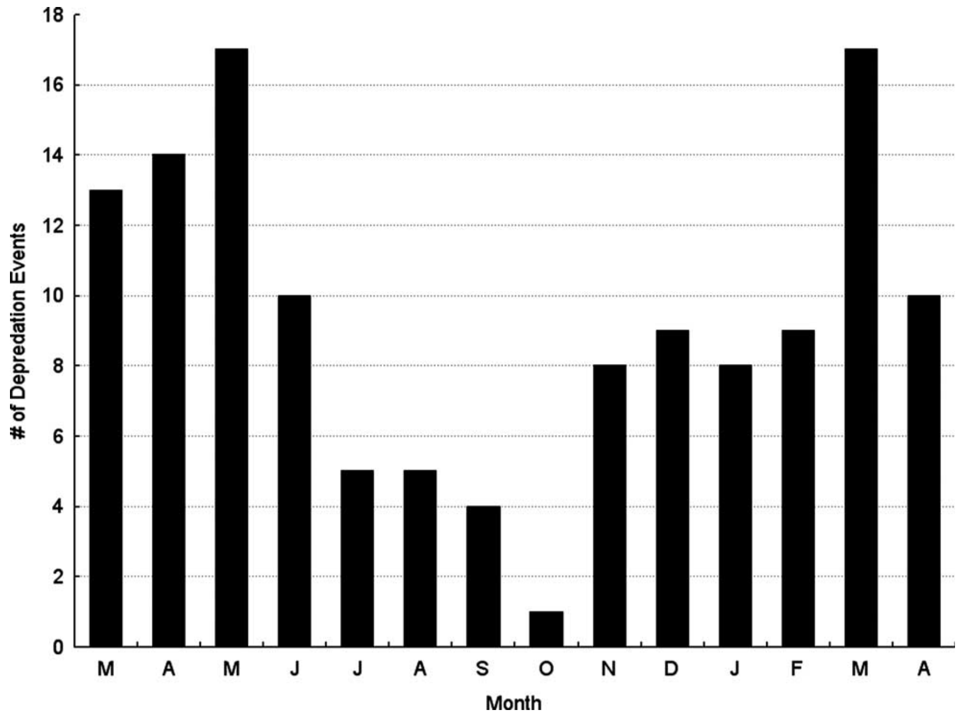

Fig. 4 – Total monthly livestock attacks by predators recorded within 2 km of the northeastern border of the Maasai Mara National Reserve, Kenya, from March 2003 to April 2004. Conflicts included attacks by lions, leopards, and hyenas that resulted in either death or injury of livestock.

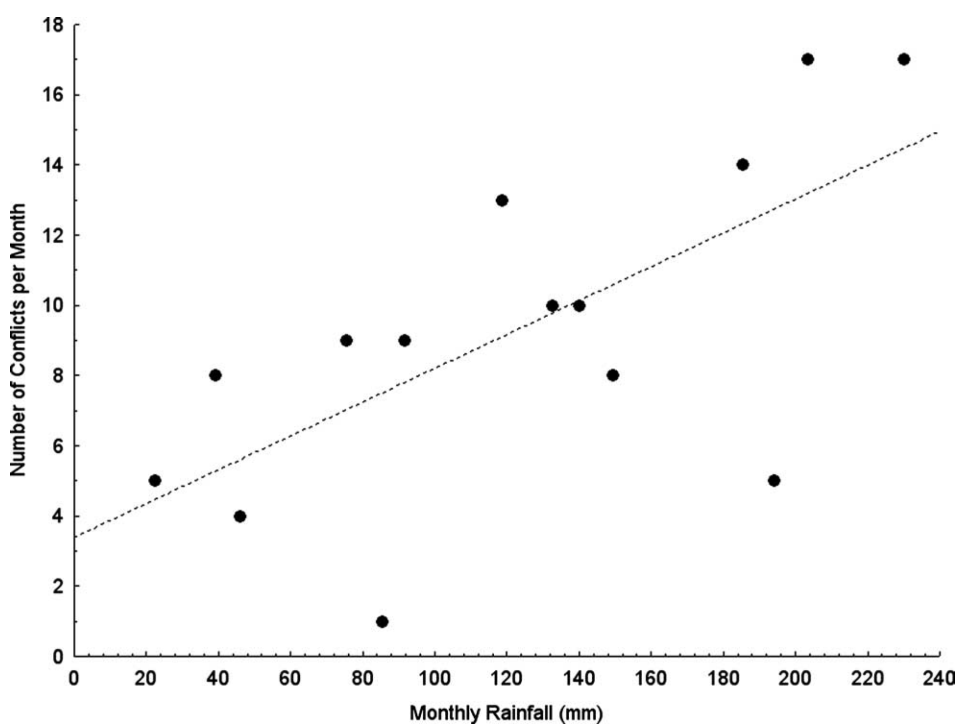

Fig. 5 – Correlation between monthly rainfall (mm) and total predator incident reports collected each month during a 14-month study period.

at least one leopard attack on livestock had fewer other bomas within a 200 m radius, and were further from the closest boma than those suffering no leopard attacks (Table 1). Enclosures attacked by hyenas were closer to the next enclosure and were more frequently constructed of local bush material than were unattacked enclosures (Table 2). Enclosures suffering

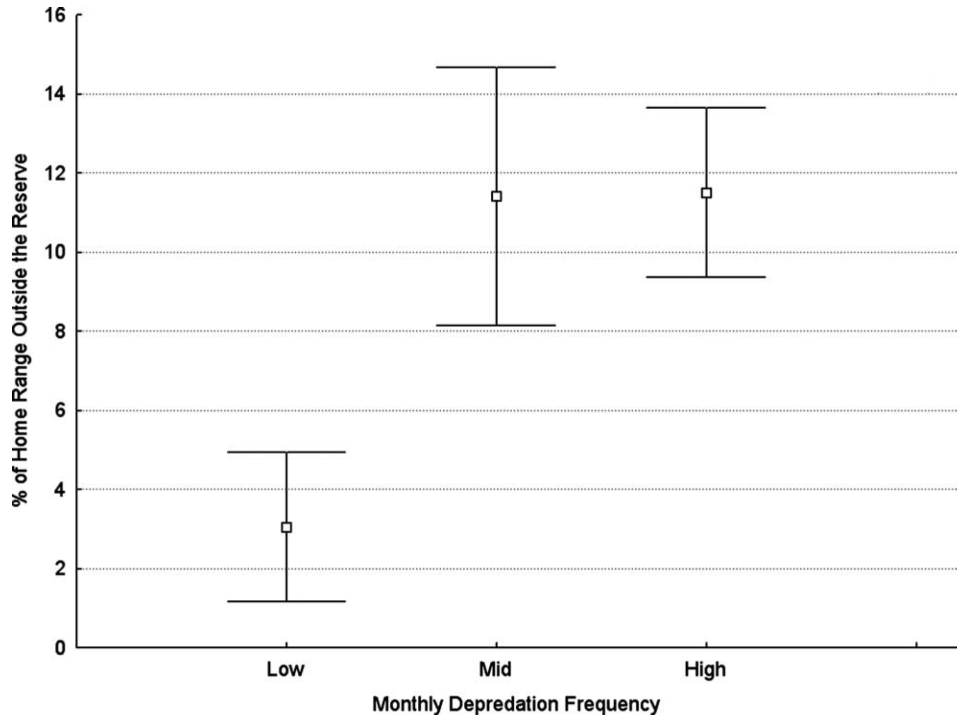

Fig. 6 – Proportion of individual hyena home ranges (95% fixed-kernel) that were located outside the Masaai Mara National Reserve during months of low, medium and high frequencies of livestock depredation events involving hyenas from March 2003 to April 2004. Whiskers indicate 95% confidence intervals.

Table 1 – Univariate comparisons between mean values ±standard error of nine independent variables recorded at attacked and unattacked Maasai bomas (villages) within 2 km of the northeastern border of the Maasai Mara National Reserve, Kenya

	N	Hyena boma attack			Leopard boma attack		
		Yes	No	*p*-Value	Yes	No	*p*-Value
Boma cows (#)	68	222.0 ± 42.1	127.4 ± 118.7	0.039[a]	189.6 ± 44.1	152.7 ± 22.4	0.420
Boma sheep/goats (#)[b]	69	349.0 ± 65.3	171.9 ± 19.0	0.010[a]	322.9 ± 66.8	206.6 ± 28.6	0.108
Boma dogs (#)[b]	67	6.6 ± 1.0	4.1 ± 0.4	0.016[a]	6.3 ± 1.2	4.5 ± 0.4	0.308
Boma houses (#)[b]	69	9.9 ± 1.2	5.2 ± 0.4	0.000[a]	8.2 ± 1.6	6.2 ± 0.5	0.299
Distance to Reserve (m)	69	731.7 ± 102.5	915.1 ± 57.7	0.075	790.7 ± 114.8	890.7 ± 57.1	0.286
Sheep/goat enclosures (#)[b]	71	1.8 ± 0.3	1.0 ± 0.0	0.022[a]	1.7 ± 0.4	1.2 ± 0.1	0.355
Distance to cover (m)	66	253.9 ± 39.3	306.5 ± 47.3	0.969	312.8 ± 69.2	280.1 ± 39.1	0.757
Bomas in 200 m (#)	69	1.8 ± 0.4	1.6 ± 0.3	0.795	0.4 ± 0.2	2.1 ± 0.3	0.003[a]
Closest boma (m)	69	230.1 ± 53.7	222.4 ± 25.9	0.651	314.7 ± 40.2	192.8 ± 29.9	0.001[a]

P-values are based on Mann–Whitney *U* tests.
Variables indicated by asterisks are intercorrelated.
a Significant at $\alpha = 0.05$.
b Intercorrelated variables.

leopard attacks only differed from unattacked enclosures with respect to fence type, with attacked enclosures more likely to be made from pole fencing than were unattacked enclosures (Table 2).

There was no difference between the proportion of pole (43%) and bush fences (36%) present in the study area that were attacked by predators (Fisher exact test, $p = 0.656$). However, sheep and goats enclosed by pole fences were more likely to be attacked by leopards than were those enclosed by bush fences (Fisher exact test, $p = 0.002$), whereas small stock within bush fences were more likely to be attacked by hyenas than were those in pole enclosures (Fisher exact test, $p = 0.003$; Fig. 7). Livestock held under strong, well-maintained pole fences were no less likely to be attacked by leopards (Fisher exact test, $p = 0.752$) or hyenas ($p = 0.286$) than were those within weak pole fences. Similarly, relative strength of bush fences did not affect probability of attack by either hyenas (Fisher exact test, $p = 0.757$) or leopards ($p = 1.0$).

3.3.2. *Multivariate analyses*

Nine variables were initially considered for estimation of hyena and leopard attack probability at bomas (Table 1). The

Table 2 – Univariate comparisons between mean values (SE) of seven independent variables recorded at attacked and unattacked sheep/goat enclosures within 2 km of the northeastern border of the Maasai Mara National Reserve, Kenya

	N	Hyena sheep/goat attack			Leopard sheep/goat attack		
		Yes	No	*p*-Value	Yes	No	*p*-Value
Sheep/goats inside (#)	99	196.3 ± 27.8	158.0 ± 14.1	0.189	205.0 ± 34.4	155.4 ± 12.7	0.281
Dogs at enclosure (#)	96	4.0 ± 0.3	3.7 ± 0.3	0.363	4.0 ± 0.5	3.7 ± 0.3	0.488
Houses at enclosure (#)	90	4.6 ± 0.4	4.9 ± 0.3	0.809	4.6 ± 0.6	4.9 ± 0.3	0.669
Enclosures in 200 m (#)	96	3.7 ± 0.6	2.9 ± 0.4	0.200	2.7 ± 0.8	3.2 ± 0.3	0.092
Closest enclosure (m)	96	116.7 ± 55.9	156.5 ± 18.6	0.013[a]	201.6 ± 41.4	131.2 ± 21.4	0.178
Pole enclosure (%)	93	18.2	50.7	0.007[a]	77.3	32.4	0.000[a]
Bush enclosure (%)	93	77.3	38.0	0.002[a]	22.7	54.9	0.014[a]

P-values are based on Mann–Whitney *U* tests for continuous variables and Fisher exact tests for proportions. None of the variables examined here were intercorrelated.
a Significant at $\alpha = 0.05$.

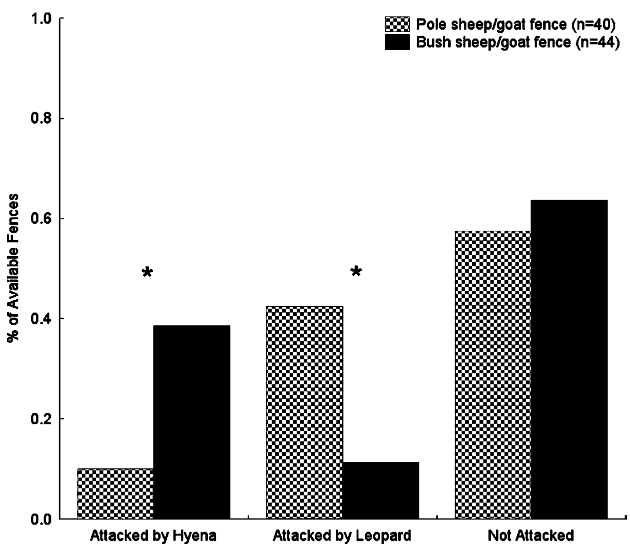

Fig. 7 – Relative attack rates by leopard and hyena on the two most common types of sheep/goat enclosures within 2 km of the northeastern Reserve border. Significant differences (Fisher exact test for comparison of proportions; $p < 0.05$) are indicated by an asterisk.

most significant of all intercorrelated variables, number of boma houses, was retained, and the remaining correlated variables were excluded from further analysis. With occurrence of a hyena attack as the dependent variable, all possible model combinations of the six remaining variables were compared based on AICc values. The lowest AICc value was assigned to a model including the number of boma houses (Wald's $\chi^2 = 13.52$; $p < 0.001$) and the distance to the Reserve (Wald's $\chi^2 = 3.92$; $p = 0.048$) as predictive variables (Log-likelihood $\chi^2 = 22.54$, $p < 0.0001$). Two additional models were supported by the data; however, none of the variables other than distance to the Reserve and the number of bomas houses were significant parameters in these additional models. Model selection procedures thus indicated that likelihood of hyena attack on bomas increased as number of houses increased and distance to the Reserve decreased.

Considering all possible models with the same six variables predicting boma attack by leopards, the lowest AICc value was assigned to a model including only the number of bomas within a 200 m radius (Wald's $\chi^2 = 7.38$, $p = 0.007$; Log-likelihood $\chi^2 = 12.17$, $p < 0.001$). Two additional models were included in the optimal subset of models; however, none of these additional models included significant parameter estimates additional to the number of bomas within 200 m. Therefore, modeling procedures indicated that a decrease in the density of surrounding bomas was the most important factor increasing the probability of a leopard attack.

In estimating the probability of leopard and hyena attacks on individual sheep/goat enclosures, both logistic regression models initially considered five continuous variables and one categorical variable representing fence type. Model-building for enclosure attack probability by hyenas indicated a set of six optimal models, with the lowest AICc value assigned to a model that included only fence type (Wald's $\chi^2 = 9.64$; $p = 0.002$) as an independent variable (Log-likelihood $\chi^2 = 6.42$, $p = 0.011$). No additional variables in the other five models were significant model parameters. The odds ratio for fence type indicated that the presence of a bush fence increased the probability of hyena attack by 2.43 times. With enclosure attack by leopards as the dependent variable, we identified five optimal models. The model with the lowest AICc only included fence type (Wald's $\chi^2 = 11.88$; $p = 0.001$) as a model variable (Log-likelihood $\chi^2 = 11.49$, $p = 0.001$), and no additional variables in the other four models were significant model parameters. The odds ratio for fence type indicated that the presence of a pole fence increased the probability of leopard attack by 2.67 times.

4. Discussion

4.1. *Predator involvement and livestock losses*

Our study was designed, in part, to complement and expand on recent work on livestock depredation by carnivores on East African rangelands. Patterson et al. (2004), who conducted their study on commercial ranches in southeastern Kenya, found lions to be responsible for 86% of attacks on livestock, with hyenas involved in <10%. They reported no leopard attacks on livestock. A study conducted primarily on commercial ranches in northern Kenya found that lions accounted for approximately 63% of all livestock kills, with hyenas and leopards accounting for only 15% and 11% of kills, respectively (Ogada et al., 2003). In a study conducted on group ranches near our own study site, Karani (1994) found that leopards were the most serious livestock predators (50% of livestock attacks), with lions and hyenas responsible for 31% and 19% of recorded attacks,respectively. Thus, although multiple studies on Kenyan rangelands concluded that lions are the most serious livestock predator, and that hyena predation is relatively infrequent (Frank, 2000; Ogada et al., 2003; Patterson et al., 2004), we found relatively little involvement by lions in livestock attacks, particularly at bomas, with leopards and hyenas responsible for most attacks.

Regional variation in relative livestock depredation by these large predators could be attributed to differences in relative densities of large carnivores, husbandry practices, or relative abundance of different stock species. Although some researchers have been unable to associate predator density with livestock depredation rates (Connor et al., 1998; Graham et al., 2005), others have clearly documented increases in livestock depredation rates with increases in carnivore density (Sagor et al., 1997; Stahl et al., 2001; Stoddart et al., 2001). Recent surveys on the Koyake group ranch have indicated that lion densities there may be very low (Ogutu et al., 2005). However we assumed at least some of our depredation events involved lions from inside the Reserve, where lion density was relatively high (0.369 lions/km^2; Ogutu et al., 2005). Hyena density in the northeastern portion of the Reserve was estimated to be 0.86/km^2 (Frank, 1986), one of the highest densities reported in Africa. Unfortunately, predator densities are not reported in most studies, preventing direct comparisons.

Husbandry practices on commercial ranches may reduce the relative involvement of hyenas in livestock depredation. Various researchers have concluded that rates of livestock loss to predators in Kenya, particularly hyenas, could be reduced through construction of sturdier boma fences (Kruuk, 1981; Frank, 2000), and bush fences for livestock corrals on commercial ranches are often sturdier than those built in pastoral bomas (Ogada et al., 2003). However, Ogada et al. (2003) found no effect of boma height or thickness on depredation rates. Our data support the conclusion that improved fencing, at least on pastoral ranches, is not necessarily an effective solution to livestock depredation.

Finally, relative availability of small and large stock animals may also influence involvement of predators in depredation. The Patterson et al. (2004) study, which reported low hyena depredation, included ranches on which the majority of stock animals were cattle (Patterson et al., 2004). The low frequency of hyena and leopard depredation in some areas may thus result from the rarity of their preferred livestock prey, sheep and goats.

The annual loss of 0.6% and 0.2% of the total small stock and cattle holdings respectively for our study region falls within the range reported for a large subset of depredation studies from around the globe (0.02–2.6% of local livestock holdings (Graham et al., 2005)). Within Kenya, reported annual livestock losses to predators range from 0.7% to 5.5% (Kruuk, 1981; Karani, 1994; Frank, 1998; Patterson et al., 2004), indicating that our observed depredation rates are relatively low for Kenyan rangelands. In contrast to Ogada et al. (2003), who found cheetah to be a significant predator of sheep and goats, we found no cheetah predation on livestock. This, together with the relatively small impact of lions on livestock, particularly sheep and goats, may account for our low depredation rates. However, these low annual stock losses to predators fail to represent the significance and costs of depredation events to individual owners, who have been known in our study area to lose up to 70 sheep and goats in a single attack by hyenas. Such a loss to an individual livestock owner is catastrophic and can also result in devastating retaliatory attacks. For example, in 1990, at least 16 hyenas were killed in a single poisoning event following a depredation incident in our study area (Holekamp and Smale, 1992). Although Kenyans are legally permitted to kill carnivores in defense of their livestock, these events are generally underreported due to fears of government fines or penalties, and likely resulted in an underestimation of carnivore losses during our study period.

4.2. *Attacks on grazing herds*

Attacks on grazing herds here were just as common as attacks at bomas. While studies on commercial ranches have found approximately 25% of livestock attacks to occur on grazing herds (Ogada et al., 2003; Patterson et al., 2004), pastoral ranches have documented up to 90% of predator attacks to be directed at grazing herds (Kruuk, 1981). Attacks on grazing herds are probably more frequent on pastoral group ranches due to differences in herdsman behavior. On commercial ranches, herders are paid for their work, may be fired for inadequate herd attendance, and work in groups large enough to discourage stock theft (Ogada et al., 2003). Larger groups of herders appear to be effective at limiting attacks on grazing herds (Ogada et al., 2003; Ikanda, 2005). Herds on pastoral ranches however, such as those included in our study, are often accompanied only by small groups of young boys who vary considerably in their level of attendance to the herd. Accounts of attacks on grazing herds in our study often described predators rapidly emerging from vegetative cover to attack. We therefore suggest that herdsmen avoid densely vegetated areas, where possible, particularly during the rains when attacks are most frequent and vegetation is thickest.

4.3. *Temporal patterns of attacks and relationship to predator movements*

Although Maasai pastoralists in some areas recognize rainy seasons as periods of increased carnivore conflict (Rudnai, 1979; Patterson et al., 2004), some previous researchers have been unable to associate rainfall with depredation frequency (Rudnai, 1979), while others have found the highest rates of depredation in the dry season (Butler, 2000; Ikanda, 2005). However, elevated rates of lion–human conflict have been associated with the monsoon rains in India (Saberwal et al., 1994), and recent studies have documented increases in livestock depredation during the rains in Africa (Patterson et al., 2004; Woodroffe and Frank, 2005). Our data further support the importance of this relationship. Both Patterson et al. (2004) and Woodroffe and Frank (2005) suggest this trend may be ultimately driven by seasonal variation in local availability of natural prey. Whether the wet or dry season brings increased depredation is then likely dictated by the regional relationship between rainfall and natural prey. Whereas the dry season in some regions is associated with increased natural prey and reduced livestock depredations, the inverse has been shown in areas where prey numbers peak in the wet season (e.g. southern Serengeti; (Ikanda, 2005)). Although our data failed to directly relate prey abundance with rainfall, prey abundance clearly influenced depredation rates. Many studies have documented relatively high rates of carnivore predation on livestock in areas occupied by few natural prey (Meriggi and Lovari, 1996; Mishra, 1997; Vos, 2000; Polisar et al., 2003; Woodroffe et al., 2005), while others have shown, as in this study, depredation rates to increase as natural prey abundance decreases (Stoddart et al., 2001).

Temporal variation in hyena depredation behavior was associated with changes in space use by monitored hyenas. As expected, hyenas used group ranch property more during months when hyena attacks on livestock were most frequent. However, the ecological conditions associated with this spatial shift were unclear. No correlation was found between either rainfall or prey abundance and the observed HR shifts. Tracking data suggested that hyenas spent more time outside the Reserve than expected based on the small proportion of the clan territory lying outside the Reserve, and that hyenas outside the Reserve were often near bomas.

4.4. *Boma and enclosure vulnerability*

Both univariate and multivariate analyses indicated that, contrary to previous findings (Ogada et al., 2003), increased human activity was associated with an increased probability of hyena attack. Based on these and follow data, we suspect that hyenas, as opportunistic feeders, are making regular visits to bomas not for livestock primarily, but rather for discarded food and other edible items. Large bomas, with more human activity, would thus be most attractive to hyenas interested in exploiting refuse and opportunistic attacks on livestock should therefore be more likely to occur at these bomas. Given the attractiveness of these sites to foraging hyenas, secure refuse disposal at bomas may reduce hyena attack frequency.

Unlike hyenas, leopards preferred to attack bomas that were relatively isolated on the landscape. Because leopards, in contrast to hyenas, generally only consume fresh meat and are not known to frequent open spaces, such as those surrounding most bomas in our study area, a leopard approaching a boma is more likely than a hyena to be searching specifically for livestock prey. While our findings suggest that leopards avoid dense aggregations of human settlements, they do not indicate leopards select smaller bomas, as did the results of Ogada et al. (2003). Our results may suggest a trade-off in boma selection by leopards. While isolated bomas offer a reduced level of human activity and thus reduced probability of predator detection, bomas with fewer enclosures or livestock offer reduced opportunities to access appropriately vulnerable prey. As in Ogada et al. (2003), our results indicated that dogs were generally ineffective in deterring leopard or hyena attacks; these were further supported by villager reports suggesting that dogs were killed and eaten by both predators with some frequency.

The only variable effective in estimating the vulnerability of sheep/goat enclosures was fence type. Overall, fences made from bush and pole material were equally susceptible to predator attack. Given that material used to make pole fences is expensive and not obtained locally, this was a surprising finding. Although pole fences require less maintenance and appear to be effective deterrents against hyena attack, the use of pole material in enclosure construction more than doubled the likelihood of a leopard attack. Although many villagers reinforced pole fences with iron sheeting, barbed wire or thorn bush to close gaps and remove possible footholds, leopards appeared capable of capitalizing on small weaknesses in these reinforcements. Although bush fences seemed effective at limiting leopard attacks, probably because they provide few sturdy footholds for climbing, the use of bush material in enclosure construction more than doubled the likelihood of a hyena attack, as hyenas proved highly adept at pushing through even the densest of bush fences.

4.5. *Conclusions*

Given the absence of a relationship between predator attack frequency and fence quality, and the time, labor, and depletion of local vegetation involved in maintaining a strong fence (Kruuk, 1981), it may be more effective for livestock owners to concentrate efforts on developing novel methods of detection and interruption of carnivore attacks, than on improving fences to minimize losses. Although our data indicate that human activity not specifically designed to deter predators may be ineffective in reducing attack probability, active guarding of bomas (e.g. posting night guards, sleeping in huts within enclosures), particularly with the help of lights, may prove effective. Investment of effort in guarding enclosures, a practice rarely utilized in our study area, would be most beneficial during the rainy season, when attacks are most common, and could likely be relaxed when migratory herds are present. Pole enclosures are effective at minimizing losses to hyenas and should therefore be used, when affordable, at larger bomas, particularly those in dense aggregations, which our data indicate are more susceptible to hyena attack. Bush fences seem to provide superior leopard exclusion and should therefore be favored at isolated bomas, which appear more vulnerable to leopard attacks. With respect to our finding that the size and isolation of a boma can influence its vulnerability to predator attack, similar findings in North America regarding wolf depredation on cattle farms (Mech et al., 2000) indicate that these factors may be important spatial predictors of livestock attacks not only by African predators, but by predators worldwide. Our study has demonstrated that monitoring of both socio-ecological and environmental variables, coupled with detailed depredation information, can be useful in generating practical recommendations for conflict mitigation. In addition, knowledge of the movements and behavior of predators involved in depredation events can offer important insight into the effectiveness of depredation prevention measures.

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